Is the nestedness of metazoan parasite assemblages of marine fishes from the southeastern Pacific coast a pattern associated with the geographical distributional range of the host?

M. T. GONZÁLEZ* *and* M. E. OLIVA

Instituto de Investigaciones Oceanológicas, Universidad de Antofagasta, Casilla 170-Antofagasta, Chile

(*Received 21 October 2008; revised 15 December and 29 December 2008; accepted 30 December 2008; first published online 6 February 2009*)

SUMMARY

Nested structure is a pattern originally described in island biogeography to characterize how a set of species is distributed among a set of islands. In parasite communities, nestedness has been intensively studied among individual fish from a locality. However, nested patterns among parasite assemblages from different host populations (localities) have scarcely been investigated. We recorded the occurrence of parasites in 9 fish species widely distributed along the southeastern Pacific coast to determine whether the ecto- and endoparasite assemblages of marine fishes show a nested structure associated with host distributional range. Nestedness was tested using Brualdi-Sanderson index of discrepancy (BR); and 5 null models incorporated in a '*Nestedness*' programme (Ulrich, 2006). The ecto- and endoparasite richness do not show similar patterns of latitudinal gradients among fish hosts, with 33–66% of analysed ectoparasite assemblages, and 25–75% of endoparasite assemblages showing nested structures through the host distributional range. For ectoparasites, species richness gradients and nested structure (when present) might be associated with decreased host densities or could reflect negative environmental conditions in the distributional border of the host species, whereas for endoparasites might be caused by geographical breaks of prey or changes in prey availability (intermediate hosts). The sampled extension of the distributional range of the host species, as well as the lack of specificity of some parasites, could influence the detection of nestedness.

Key words: biogeography, Chile, marine fishes, nested patterns, Peru, species richness.

INTRODUCTION

Spatial ecology is one of the great advances of modern population and community ecology, which has highlighted the importance of the spatial scale for understanding a wide range of ecological phenomena (Holt, 2000). Currently, some parasite ecologists have attempted to explain the parasite distributional patterns (abundances and species richness) on various spatial and temporal scales through different ecological models derived from those developed for free-living organisms (e.g. Rohde *et al*. 1998; Gotelli and Rohde, 2002; Poulin, 2004). However, there is no consensus regarding whether there are general patterns in parasite communities (Poulin, 2007*a*). To date, most efforts in parasite community studies have been focused on determining distributional patterns in the abundances or species richness (references in Poulin, 2007*a*, *b*). Early predictions were based on the theory of island biogeography (Kuris *et al*. 1980) and, more recently, empirical tests show that epidemiological processes may be important as a determinant of local parasite species richness (Morand and Poulin, 1998). In contrast, patterns in community composition (taxonomic identity) have been by far less analysed. Presence/absence matrices of sites versus species records, with species being present or absent at each site, are commonly recorded and potentially give valuable distributional information about species, communities, and environments (Wright *et al*. 1998).

Nested structure is a pattern originally described in island biogeography to characterize how a set of species is distributed among a set of islands (Patterson and Atmar, 1986). A nested pattern has been defined as a departure from a random association of species in which species that compose a depauperate island community constitute a proper subset of those species inhabiting richer islands (Atmar and Patterson, 1993). In order to detect community structure, this pattern has also been investigated in other ecological systems such as mountains, ponds, streams, and fragmented forest patches (references in Fischer and Lindermayer, 2005). Nestedness has also been recorded for parasite species among conspecific host individuals (=infracommunities) from a locality, but these results differ according to the host species studied (Rohde *et al*. 1998; Poulin, 2007*a*), which could be a consequence

---

* Corresponding author: Tel: +56 55 637404. Fax: +56 55 637804. E-mail: mtgonzalez@uantof.cl

Parasitology (2009), **136**, 401–409.
doi:10.1017/S0031182009005575 Printed in the United Kingdom

of the different methods applied to evaluate nestedness in those host-parasite systems (Timi and Poulin, 2008). Individual hosts represent replicated habitats in time and space, allowing consideration of them as a unit of study in the context of island biogeography theory (Kuris, 1980). However, at this local scale (individual hosts), there are several other non-biogeographical factors (i.e. fish size range, differential food consumption rate, differential susceptibility, etc) than can cause nestedness (Morand *et al*. 2002). The geographical distributional patterns of parasites are directly associated with host distributional range, which are influenced at the same time by biogeographical processes such as dispersal abilities of parasites and hosts, and by prey geographical distributions or prey availabilities (intermediate hosts), which is in agreement with the original idea of the nested subset patterns developed by Patterson and Atmar (1986). Thus, nested patterns in parasite communities should be sought on a larger geographical scale, that is, across different localities or host populations (=component communities *sensu* Bush *et al*. 1997). The nestedness patterns associated with distributional range in parasites of rodents have been investigated (Goüy de Bellocq *et al*. 2003; Krasnov *et al*. 2005). However, to date, there is only a single study that analyses the nestedness in parasite communities of the same marine fish host across its geographical range (González and Poulin, 2005). Therefore, more investigations are necessary to determine if the nestedness pattern of parasite assemblages of the same host species could be a pattern associated with the geographical distributional range of the host.

The distributional patterns of marine parasites may be determined by oceanographic characteristics (temperature, depth, specific water masses) and also by factors associated with the hosts (density, feeding habits and migratory patterns) (Bush *et al*. 2001). Along the Chilean coast, 2 faunistic provinces are generally recognized: the Peruvian faunistic province, extending from Peru to the northern Chilean coast (*ca*. 30°S), and the Magellanic faunistic province, extending southward of 42°S along the southern Chilean coast. Between both areas lies a transitional zone where species of northern and southern origin overlap (Briggs, 1974; Lancellotti and Vásquez, 1999). Therefore, it is expected that parasite assemblages show nested structure across host populations of fish species with an extensive geographical distributional range. Nestedness in those parasite communities could be produced by environmental factors (which could limit the survival of ectoparasites), and by changes in the prey availability (intermediate hosts) along their distributional range. Thus, the aim of this study was to determine whether assemblages of ectoparasites and endoparasites – analysed separately – of several marine fishes with an extended geographical distribution in the south-eastern Pacific show a nested structure, which could be associated with extrinsic factors associated to host species distributions.

MATERIALS AND METHODS

Specimens of *Pinguipes chilensis, Prolatilus jugularis, Scomber japonicus, Nezumia pulchella* and *Hippoglossina macrops* were captured from different latitudes along the southeastern Pacific coast from March to June 2006 and from February to May 2007 (Fig. 1). The first 3 fish species were collected either by hand line, speared by divers, or they were acquired from local fishermen. The 2 deep-sea fish species were captured as by-catch from the shrimp fishery. The samples were captured in the same period of year to avoid seasonal influence on the composition of parasites in the fish hosts. Additionally, we used our own data base for parasites of *Sebastes capensis, Trachurus symmetricus, Engraulis ringens* and *Merluccius gayi*. Sampled latitudes, sample sizes, and host habitat are given in Table 1.

The total length (TL) of each fish was measured (to ±1 cm) prior to dissections. Ectoparasites and endoparasites were collected using standard parasitological techniques outlined by González and Acuña (1998). The collected parasites were sorted, counted, and preserved in 70% ethanol for identification. The specialized literature was used to identify each parasite species.

For each parasite species, prevalence (=number of fish infected with a particular parasite species divided by the number of fish examined) was estimated according to Bush *et al*. (1997). Parasite richness (number of ectoparasite or endoparasite species present in each component community *sensu* Bush *et al*. 1997) was calculated for each locality. Because sampling effort and host sizes may exert a strong bias in parasite species richness estimation across different localities (Poulin, 2007*b*), Spearman correlation matrices were used to evaluate the relationships among sample size, mean host size, latitude and species richness for each fish host species (Zar, 1999). Subsequently, meta-analyses for correlation data using fixed and randomized effects models were performed by Comprehensive Meta-Analysis (CMA) program (www.Meta-Analysis.com).

Nested subset analyses were carried out separately for ecto- and endoparasite component communities of each host species. First, the analyses were performed considering all recorded parasites, and then including only the parasite species with prevalence >5% in at least 1 locality. Patterns of nestedness using the software *Nestedness* were evaluated (Ulrich, 2006). This program includes 6 null models, and different nestedness indices. The FF (fixed row and fixed column) null model has been demonstrated to be the most conservative; and among the indices, the Brualdi and Sanderson discrepancy index (BR) of

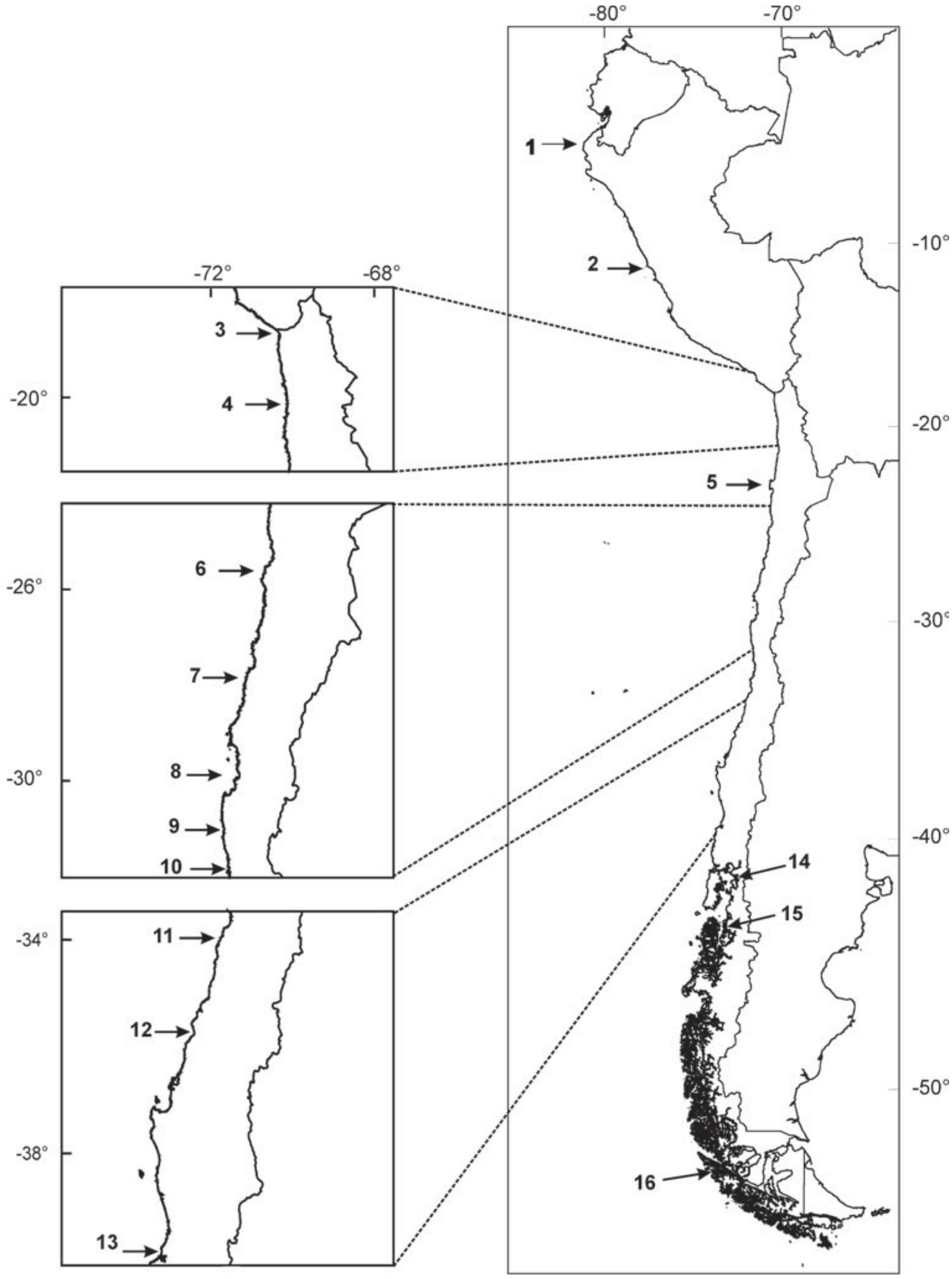


Fig. 1. Approximate position of sampled localities. Code for locality: 1 = Paita, 2 = Callao, 3 = Arica, 4 = Iquique, 5 = Antofagasta, 6 = Caldera, 7 = Huasco, 8 = Coquimbo, 9 = El Teniente, 10 = Valparaíso, 11 = Bucanero, 12 = Talcahuano, 13 = Valdivia, 14 = Puerto Montt, 15 = Aysén, 16 = Punta Arenas.

unexpected presences was the best in the performance, according to Ulrich and Gotelli (2007*a*, *b*). Then the BR index was used because data-base matrix properties did not influence it. The FF algorithm is not recommended for matrices that are 'evidently' nested. In these matrices, the Z score value is zero because there is no analysis performed. So, the FF algorithm cannot be used in a perfectly nested matrix because there are no possible matrix rearrangements to maintain fixed row and column addition (Ulrich and Gotelli, 2007*a*). Since different null models may give different results, 5 null models for presence-absence data: FF (fixed row and fixed column totals), FE (fixed row totals, equiprobable column totals), EF (equiprobable row totals, fixed column totals), EE (equiprobable row totals and equiprobable column totals), PE (proportional row totals, equiprobable column) were used. To compute the null models, we used default values for randomizations (= 100), cell minimum distance to the border line (= 0·5), and matrices were randomized by species richness. Additionally, we evaluated nestedness using the option 'unsorted matrix', which is helpful in studies of gradients that might influence the degree of nestedness (Ulrich, 2006). However, we did not find significant differences using either option.

Table 1. Ectoparasite (left value) and endoparasite (right value) species richness of the component communities from the different fish species

(In parenthesis, sample size. Habitat/habits: ^{a} Benthic/non-migratory; ^{b} demersal/non-migratory; ^{c} demersal/migratory; ^{d} pelagic/migratory; ^{e} pelagic/non-migratory; * no data.)

Latitude	*Sebastes capensis*^{a}	*Pinguipes chilensis*^{a}	*Prolatilus jugularis*^{a}	*Nezumia pulchella*^{b}	*Hippoglossina macrops*^{b}	*Merluccius gayi*^{c}	*Trachurus symmetricus*^{d}	*Engraulis ringens*^{d}	*Scomber japonicus*^{e}
5°S							4–1 (105)		
11°S	*–4 (50)						2–1 (122)		5–4 (60)
18°S							2–5 (117)	3–1 (60)	
20°S	4–3 (55)	4–8 (51)					2–8 (111)		
24°S	7–7 (67)	5–11 (46)	6–13 (46)	5–10 (50)	3–4 (34)		2–7 (110)	3–3 (60)	6–7 (60)
26°S				4–8 (40)	3–8 (29)			3–4 (60)	
28°S				4–4 (25)	4–9 (76)				
30°S	9–8 (61)	5–11 (51)	10–11 (50)	4–4 (29)	5–9 (60)	3–12 (194)	2–3 (106)	3–3 (60)	4–3 (60)
31°S				2–4 (23)					
32°S	9–7(50)			1–4 (50)	4–7 (50)	5–14 (205)		1–2 (60)	
34°S					4–5 (30)				
36°S	10–11 (71)	9–8 (45)	8–11 (50)		5–7 (50)	3–13 (198)	2–6 (108)	0–2 (60)	3–4 (30)
40°S	9–14 (67)		7–13 (46)			4–10 (185)			
42°S		7–4 (50)							
45°S	6–8 (79)	5–3 (50)	2–7 (26)						
52°S	4–10 (37)								

Nestedness significance levels were obtained from Z-scores, and lower and upper 95% confidence limits of the respective null model distributions (Ulrich, 2006; Ulrich and Gotelli, 2007*a*).

RESULTS

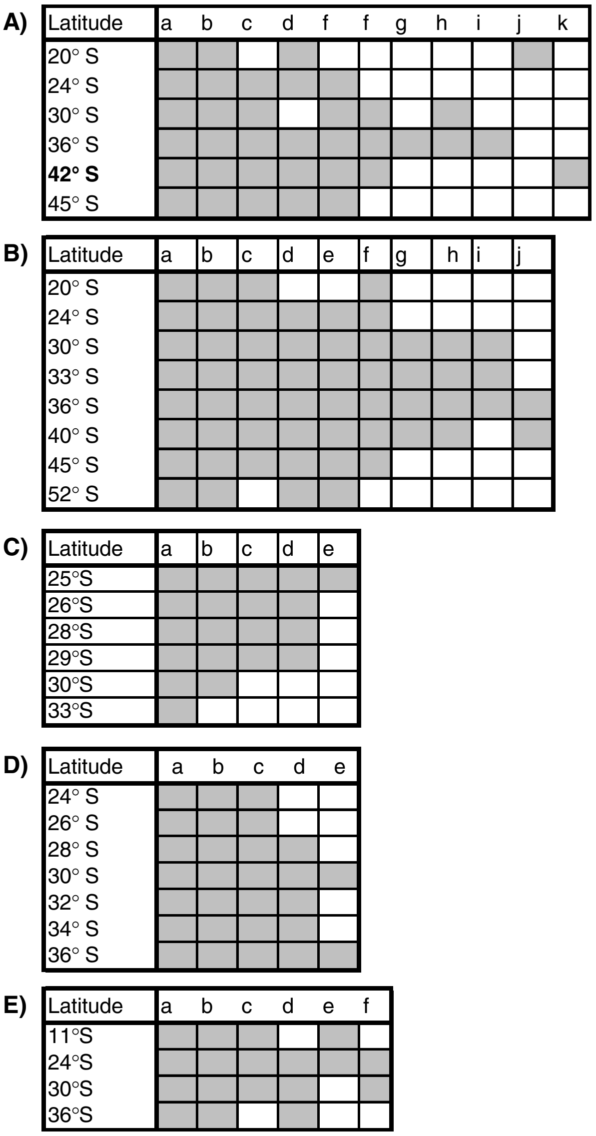
The fish species studied harboured between 3 and 12 ectoparasites and between 3 and 29 endoparasite species (Table 1). *Engraulis ringens* harboured only 2 ecto- and 2 endoparasite species with prevalences higher than 5%. Similarly, *Merluccius gayi* harboured only 3 ectoparasite species with prevalence >5%, and *Trachurus symmetricus* harboured only 4 ectoparasite species, 2 of them present in all localities and the other 2 present only in 1 locality (Table 1). Therefore, as those hosts harboured few parasites, nestedness was not evaluated for ectoparasites of *E. ringens, M. gayi* and *T. symmetricus*, and for endoparasites of *E. ringens*. In the remaining fish hosts, the ectoparasite richness did not show common latitudinal gradients (Table 1; Figs 2 and 3). Among conspecific populations, ectoparasite richness decreased with latitude in *Nezumia pulchella* (Fig. 2C), but richness increased with latitude in *Hippoglossina macrops* (Fig. 2D). Similarly, the endoparasite richness increased with latitude in *Sebastes capensis* (Fig. 3B), but it decreased with latitude in *N. pulchella* (Fig. 3C). Meta-analyses of correlations showed that both ecto- and endoparasite species richness were not significantly correlated with sample size by locality, mean fish sizes or latitude ($P > 0{\cdot}05$ for all correlations; Table 2). However, the heterogeneity tests indicated that the studied hosts do not share a common effect size (Table 2).

Nested pattern detection was influenced by the null model. According to the FF null model, none of the analysed ectoparasite assemblages showed a nested structure across the latitudinal range of their hosts (Table 3), but the FF algorithm was not useful to evaluate nestedness for ectoparasites of *N. pulchella* and *H. macrops*. In the other extreme, according to the EF and EE null models only *Prolatilus jugularis* and *Scomber japonicus* ectoparasites were not nested (Table 3; Fig. 1). However, according to the PE null model only the ectoparasites of these two last hosts were nested. For ectoparasites, nested analyses results were not influenced by parasite inclusion or exclusion with a prevalence of less than 5%.

According to the FF null model, among endoparasite assemblages only *T. symmetricus* showed a nested structure (Table 4). However, nested analyses based on EF and EE null models (including all endoparasites) showed that only *Pinguipes chilensis* and *P. jugularis* were not nested through their host latitudinal range (Table 4; Fig. 3). In *P. jugularis, H. macrops* and *S. japonicus*, parasite exclusion with a prevalence <5% influenced the results of nestedness in different ways (Table 4).

DISCUSSION

González and Poulin (2005) have demonstrated that parasite communities of a marine fish (*S. capensis*) extensively distributed along the Southeastern Pacific coast (more than 44 degrees of latitude) showed significant nested patterns. However, the type of nestedness pattern differed between ectoparasites and endoparasites. In our study, migratory



A)

Latitude	a	b	c	d	f	f	g	h	i	j	k
20° S	■	■		■						■	
24° S	■	■	■	■	■						
30° S	■	■	■		■	■		■			
36° S	■	■	■	■	■	■	■	■	■		
42° S	■	■	■	■	■	■					■
45° S	■	■	■	■	■						

B)

Latitude	a	b	c	d	e	f	g	h	i	j
20° S	■	■	■			■				
24° S	■	■	■	■	■	■				
30° S	■	■	■	■	■	■	■	■	■	
33° S	■	■	■	■	■	■	■	■	■	
36° S	■	■	■	■	■	■	■	■	■	■
40° S	■	■	■	■	■	■	■	■		■
45° S	■	■	■	■	■	■				
52° S	■	■		■	■					

C)

Latitude	a	b	c	d	e
25°S	■	■	■	■	■
26°S	■	■	■	■	
28°S	■	■	■	■	
29°S	■	■	■	■	
30°S	■	■			
33°S	■				

D)

Latitude	a	b	c	d	e
24° S	■	■	■		
26° S	■	■	■		
28° S	■	■	■	■	
30° S	■	■	■	■	■
32° S	■	■	■	■	
34° S	■	■	■	■	
36° S	■	■	■	■	■

E)

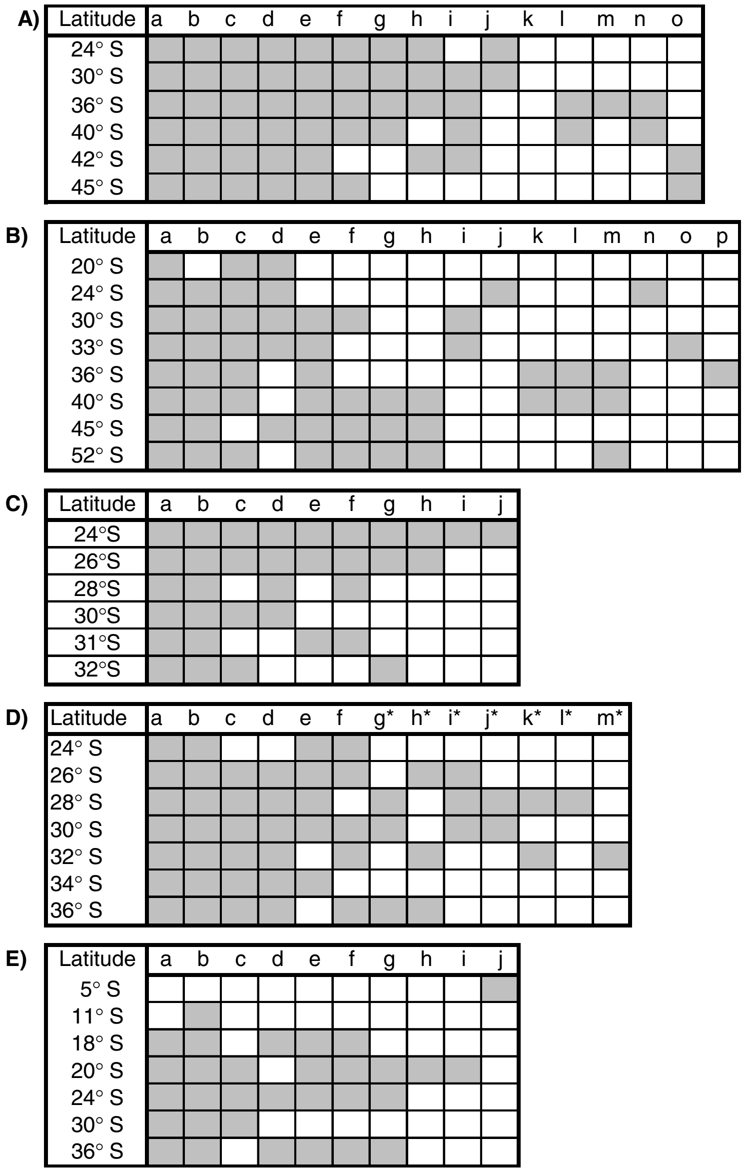
Latitude	a	b	c	d	e	f
11°S	■	■	■		■	
24°S	■	■	■	■	■	■
30°S	■	■	■	■		■
36°S	■	■		■		

Fig. 2. Matrix presence (dark square) and absence (white square) of the ectoparasites recovered across the host latitudinal range. (A) *Pinguipes chilensis*. a: *Lepeophtheirus mugiloides*; b: *Caligus cheilodactylus*, c: *Paramicrocotyle* sp. d: *Neobenedenia* sp.; e: *Chalguacotyle* sp., f: *Gnathia* sp., g: *Piscicolidae* gen sp., h: *Cirolana* sp.; i: *Cimothoa* sp.; j: *Rocinela* sp., k: *Udonella australis*. (B) *Sebastes capensis*. a: *Caligus cheilodactylus*; b: *Microcotyle* sp.1; c: *Lepeophtheirus chilensis*; d: *Gnathia* sp.; e: *Interniloculus chilensis*; f: *Neobenedenia* sp.; g: *Udonella australis*; h: Piscicolidae gen. sp.; i: *Cirolana* sp.; j:*Microcotyle* sp.2; k: *Rocinela* sp. (C) *Nezumia pulchella*. a: *Jusheyhoea macroura;* b: *Diclidophora* sp.; c: *Clavella* sp1; d: *Clavella* sp2; e: *Lophoura* sp. (D) *Hippoglossina macrops*. a: *Holobomolochus chilensis;* b: *Protochondria longicauda;* *c: Neoheterobothrium chilensis;* d: *Glyptonobdella* sp.; e: *Entobdella* sp. (E) *Scomber japonicus*. a: *Kuhnia sprostonae*: b: *K. scombri*; c: *Ceratothoa* sp.; d: *Rocinela* sp.; e: *Clavella* sp.; f: *Caligus bonito*.

fish species (*M. gayi, T. symmetricus*, and *E. ringens*) harboured few ectoparasite species, which were present in the different sampled latitudes, whereas non-migratory fish species (*S. capensis, P. chilensis, P. jugularis, H. macrops* and *N. pulchella*) showed ectoparasite richness gradients along the distributional range of the hosts. However, gradients in ectoparasite richness were not correlated with latitude. On the other hand, the endoparasite richness of *S. capensis* increased with latitude, but the parasite richness of *N. pulchella* decreased. Therefore, ecto- and endoparasite assemblages of marine fishes from the Southeastern Pacific coast do not show general latitudinal patterns in parasite richness as has been previously reported (Rohde, 2005).

The detection of nestedness in binary presence-absence matrices is affected by both the metric used to quantify nestedness and the reference null model distribution. According to Ulrich and Gotelli (2007*a, b*), the best performing algorithm maintains fixed row and fixed column totals, but it is conservative and may not always detect nestedness when it is present. Therefore, when one matrix shows an evident nested pattern it is better to use an alternative null model such as EE, FE or EF (see Ulrich and Gotelli, 2007*a* for explanations about algorithms). Likewise, among the metrics of nestedness, the Brualdi and Sanderson discrepancy index (BR) performs better because it is less affected by matrix properties (that is, shape, size, fill and richness differences), which was confirmed in our data base. Taking into account the analysed matrices characteristics of this study and null model election, ectoparasite assemblage nestedness frequency in analysed marine fishes could be between 33 and 66%, whereas nested structure detection in endoparasite assemblages through the distributional range of their host could vary between 25 and 75%.

Several studies have emphasized the importance of host geographical distribution on the patterns of parasite species richness (Poulin, 2007*b*). Thus, the sampled extension of the distributional range of the hosts as well as the lack of specificity of some parasites could influence their parasite species richness and the nestedness structure (González and Poulin, 2005; González and Oliva, 2006). Three fish species, *S. capensis, P. chilensis* and *P. jugularis*, inhabit shallow waters, and are distributed approximately between 11°S and 50°S in the Southeastern Pacific coast (Pequeño, 1989). In these 3 host species the ectoparasite assemblages are richest at latitudes associated to the transitional area (30°S–40°S). These fish species share some parasites such as the cirolanid isopods, and *Gnathia* sp., the copepod *Caligus cheilodactylus*, the monogeneans *Udonella australe* and *Neobenedenia* sp. Thus, it is possible that the presence of these parasite species in intermediate latitudes could be influenced by the presence (or abundance) of some of these 3 host fish species (González and Poulin, 2005). On the other hand, parasites of the deep-water fishes *N. pulchella* and *H. macrops*, are most host-specific, and there are no shared parasite species amongst them. *N. pulchella* is



A)

Latitude	a	b	c	d	e	f	g	h	i	j	k	l	m	n	o
24° S	■	■	■	■	■	■	■	■	□	■	□	□	□	□	□
30° S	■	■	■	■	■	■	■	■	■	■	□	□	□	□	□
36° S	■	■	■	■	■	■	■	■	■	□	□	■	■	■	□
40° S	■	■	■	■	■	■	■	□	■	□	□	■	□	■	□
42° S	■	■	■	■	■	□	□	■	■	□	□	□	□	□	■
45° S	■	■	■	■	■	■	□	□	□	□	□	□	□	□	■

B)

Latitude	a	b	c	d	e	f	g	h	i	j	k	l	m	n	o	p
20° S	■	□	■	■	□	□	□	□	□	□	□	□	□	□	□	□
24° S	■	■	■	■	□	□	□	□	□	■	□	□	□	■	□	□
30° S	■	■	■	■	■	■	□	□	■	□	□	□	□	□	□	□
33° S	■	■	■	■	■	□	□	□	■	□	□	□	□	□	■	□
36° S	■	■	■	□	■	□	□	□	□	□	■	■	■	□	□	■
40° S	■	■	■	□	■	■	■	■	□	□	■	■	■	□	□	□
45° S	■	■	□	■	■	■	■	■	□	□	□	□	□	□	□	□
52° S	■	■	■	□	■	■	■	■	□	□	□	□	■	□	□	□

C)

Latitude	a	b	c	d	e	f	g	h	i	j
24°S	■	■	■	■	■	■	■	■	■	■
26°S	■	■	■	■	■	■	■	■	□	□
28°S	■	■	□	■	□	■	□	□	□	□
30°S	■	■	■	■	□	□	□	□	□	□
31°S	■	■	□	□	■	■	□	□	□	□
32°S	■	■	■	□	□	□	■	□	□	□

D)

Latitude	a	b	c	d	e	f	g*	h*	i*	j*	k*	l*	m*
24° S	■	■	□	□	■	■	□	□	□	□	□	□	□
26° S	■	■	■	■	■	■	□	■	■	□	□	□	□
28° S	■	■	■	■	■	□	■	□	■	■	■	■	□
30° S	■	■	■	■	■	■	■	□	■	■	□	□	□
32° S	■	■	■	■	□	■	□	■	□	□	■	□	■
34° S	■	■	■	■	■	□	□	□	□	□	□	□	□
36° S	■	■	■	■	□	■	■	■	□	□	□	□	□

E)

Latitude	a	b	c	d	e	f	g	h	i	j
5° S	□	□	□	□	□	□	□	□	□	■
11° S	□	■	□	□	□	□	□	□	□	□
18° S	■	■	□	■	■	■	□	□	□	□
20° S	■	■	■	□	■	■	■	■	■	□
24° S	■	■	■	■	■	■	■	□	□	□
30° S	■	■	■	□	□	□	□	□	□	□
36° S	■	■	□	■	■	■	■	□	□	□

Fig. 3. Matrix presence (dark square) and absence (white square) of the endoparasites recovered across the host latitudinal range. * Species with prevalence < 5%. (A) *Prolatilus jugularis*. a: *C. australe*; b: *Neoleburia georgenascimentoi ;* c) *Phyllodistomum* sp.; d: *Anisakis* sp.; e: *Cucullanus* sp.; f) *Dichelyne* sp.; g: Echinorhynchidae gen. sp., h: *Phillometra*; i: *Aporocotyle* sp.; j: Lecithastheridae gen. sp.; k: *Ascarophis* sp., l: *Nybelinea* sp.; m: *Contracaecum* sp.; n: *Lecithochirium* sp.; o: *Hysterothylacium aduncum*. (B) *Sebastes capensis*. a: *Ascarophis cf. sebastodis*; b: *Anisakis* sp., c: *Corynosoma australe*; d: *Pseudopecoelus* sp.; e: *Psettarium* sp.; f: *Hysherothylacium* sp.; g: *Cucullanus* sp.; h: *Lecithochirium genypteri*; i: *Helicometrina nimia*; j: Zoogonidae gen. sp; k: Hemiuridae gen. sp.; l: *Scolex pleuronectis*; m, n, o: Lecithastheridae spp.; p, q: Digenea spp. (C) *Nezumia pulchella*. a*:* *Lepidapedon* sp.; b: *Anisakis* sp.; c: Bucephalidae gen. sp.; d: *C. australe*; e: Hemiuridae gen. sp.; f: *Contracaecum* sp.; g: *Capillaria* sp.; h: *H. aduncum*; i: *Proleptus* sp.; j: Cystidicolidae gen sp. (D) *Hippoglossina macrops*. a: *C. australe*; b:*Neobothriocephalus aspinosus*; c: *Floridosentis* sp.; d: *Anisakis* sp.; e: *Nybelinea* sp.; f: *Scolex pleuronectis*; g*: *Bolbosoma sp.*; h*: *Philometra* sp.; i*: *Lecithochirium* sp1; j*: *Hemiuridae gen.* sp.; k*: *Arhythmorhynchus* sp.; l*: *Lecithochirium* sp2; m*: *Lecitophyllum* sp. (E) *Trachurus symmetricus*- a: *Radinorhynchus trichiuri*; b: *A. simplex*; c: *A. physeteri*; d: *Hysterothylacium* sp.; e: Larva Anisakidae; f: *Tentacularia coryphaenae*; g: *Nybelinea* sp.; h: Anisakidae sp.; i: *Scolex pleuronectis*; j: *Eutetrarhynchus* sp.

distributed between 7°S to 34°S (Pequeño, 1989), but we sampled approximately from the centre toward the southern limit of its distributional range only (24°S–33°S). In this host species, many parasite species were lost from their central distributional range toward southern latitudes. The distribution of *H. macrops* is not well known, but may extend from Perú to 47°S on the Chilean coast (Ojeda *et al.* 2000). Although we sampled a limited portion of their geographical range (25°S to 37°S), the loss of 2 ectoparasite species was observed northward of 28°S. Therefore, those non-migratory host fishes share a

Table 2. Results of meta-analyses for correlations data

(Test for effect size and 95% confidence intervals; Z value (= Fisher' Z/Standard Error) and *P* value associated to respective null hypotheses. Also given are test of heterogeneity, Q-values, degree of freedom (D.F.), and *P* values.)

Model		Effect size and 95% IC			Test of null (2 tail)		Heterogeneity							
Model	N° studies	Point estimate	Lower limit	Upper limit	Z value	*P* Value	Q value	D.F. (Q)	*P* value	I Sq	Tau Sq	Tau SE	Var	Tau
Ectoparasites *vs* latitude														
Fixed	9	−0·27	−0·58	0·11	−1·42	0·15	20·60	8	0·01	61·1	0·56	0·47	0·22	0·75
Random	9	−0·32	−0·75	0·30	−1·03	0·31								
Ectoparasites *vs* mean fish size														
Fixed	9	0·33	−0·04	0·62	1·76	0·08	12·52	8	0·13	36·1	0·20	0·28	0·08	0·45
Random	9	0·29	−0·19	0·66	1·19	0·24								
Ectoparasite *vs* sample size														
Fixed	8	0·37	−0·01	0·65	1·92	0·06	12·30	7	0·09	43·0	0·25	0·31	0·10	0·50
Random	8	0·38	−0·13	0·73	1·48	0·14								
Endoparasites *vs* latitude														
Fixed	9	0·15	−0·22	0·49	0·79	0·43	26·78	8	<0·01	70·1	0·81	0·61	0·37	0·90
Random	9	−0·06	−0·66	0·58	−0·17	0·86								
Endoparasites *vs* mean fish size														
Fixed	9	−0·24	−0·55	0·13	−1·26	0·21	13·68	8	0·09	41·5	0·24	0·30	0·09	0·49
Random	9	−0·28	−0·67	0·22	−1·11	0·27								
Endoparasite *vs* sample size														
Fixed	7	0·30	−0·09	0·60	1·53	0·13	1·31	6	0·97	0·00	0·00	0·17	0·03	0·00
Random	7	0·30	−0·09	0·60	1·53	0·13								

Table 3. Summary of nestedness analyses for ectoparasite assemblages of analysed marine fishes from the Southeastern Pacific Coast, using five null models and BR index (Ulrich, 2006)

(Given are Z-scores of BR-index for each null model, number of parasite species (spp), sites, and matrix fill (Fill) Significances are marked in bold.)

Fish host species	Spp	Sites	Fill	FF	EF	FE	EE	PE
Prolatilus jugularis	12	5	0·55	0·49	−0·38	**−2·08**	−1·92	**3·19**
Pinguipes chilensis	11	6	0·53	0·45	**−3·26**	−0·5	**−3·34**	1·34
Sebastes capensis	11	8	0·66	−0·94	**−4·33**	**−2·96**	**−5·59**	−1·05
Nezumia pulchella	5	6	0·67	0	**−3·30**	**−2·80**	**−3·05**	−0·78
Hippoglossina macrops	6	7	0·69	0	**−5·03**	−1·63	**−4·31**	0
Scomber japonicus	6	4	0·75	1·53	0·49	0·16	−0·01	**2·23**

Table 4. Summary of nestedness analyses for endoparasite assemblages of analysed marine fishes from the Southeastern Pacific Coast, using five null models and BR index (Ulrich, 2006)

(Given Z-scores of BR-index for each null model, number of parasite species (spp), sites, matrix fill (Fill). Significances are marked in bold (−2·0>Z-scores >2·0).)

Fish host species	spp	sites	Fill	FF	EF	FE	EE	PE
Prolatilus jugularis	17	5	0·61	−0·91	−1·87	−0·92	−1·74	**2·81**
Prolatilus jugularis	15	5	0·67	−1·80	**−4·59**	−1·69	**−3·98**	0·23
Pinguipes chilensis	21	6	0·38	−0·78	−0·49	**−2·13**	−1·46	**3·90**
Pinguipes chilensis	11	6	0·48	−0·54	−1·18	**−2·61**	**−2·43**	**2·33**
Sebastes capensis	29	9	0·27	−0·76	**−4·61**	−1·65	**−6·21**	**2·49**
Sebastes capensis	19	9	0·37	−1·05	**−5·51**	−1·82	**−5·80**	**2·24**
Nezumia pulchella	10	6	0·57	0	**−2·84**	**−2·64**	**−3·46**	−0·03
Hippoglossina macrops	13	7	0·56	−0·40	**−3·31**	−0·95	**−3·59**	1·23
Hippoglossina macrops	6	7	0·86	−0·27	0·28	0·44	0·57	0·25
Merluccius gayi	16	4	0·77	0·19	**−2·67**	−0·82	**−2·84**	0·58
Merluccius gayi	13	4	0·81	0	**−3·72**	0·16	**−3·14**	−0·39
Trachurus symmetricus	10	7	0·44	**−2·42**	**−3·39**	**−4·92**	**−3·95**	0·54
Scomber japonicus	12	4	0·46	−1·68	**−2·55**	**−2·75**	**−2·58**	1·78
Scomber japonicus	9	4	0·53	−0·98	−1·77	−0·49	−1·15	**3·08**

similar characteristic, that is, their ectoparasite assemblages are richest in host populations located in the central geographical distribution of the host species. This pattern might be concordant with the 'abundant centre' distribution rule (Sagarin and Gaines, 2002) because the higher ectoparasite species richness in central populations of marine fishes from the Southeastern-Pacific could reflect the optimal environmental conditions at the distributional centre of these host species. High abundances (or densities) of host species would facilitate the transmission rates of parasite species, which could cause nested patterns. Additionally, host specificity might determine whether a parasite is able to colonize a host and may be a factor that could influence nestedness structure in parasite communities (Matejusová *et al*. 2000). However, it is possible that generalist parasites could be distributed evenly among ranges of host species too, producing predictable parasite communities within and between these hosts (González and Oliva, 2006).

Different oceanographic conditions are present along the southeastern Pacific coast (Escribano and Hidalgo, 2001; Silva and Calvete, 2002). These differences do not interrupt the distributional range of the 3 benthic fish species (*S. capensis, P. jugularis* and *P. chilensis*); however, the distributions of a few ectoparasite species (i.e., Piscicolidae spp., *U. australe*, *Cirolana* sp.) seem to be restricted at some localities from the transitional area. The dispersion of those host-specific ectoparasites can be considered to be entirely dependent on their particular hosts, because they have direct life cycles and a minimal opportunity to disperse to new regions during their typically brief free-living stage (Hayward, 1997). Then, the loss of these parasite species from their hosts could be explained by environmental characteristics associated with biogeograpical areas northward and southward of the transitional area, which could limit whether the dispersion of the infested host fish populations or survival of different stages of the life cycle of some ectoparasites. A similar pattern was suggested by Krasnov *et al*. (2005), but in other host-parasite systems (Rodentia and Insectivora-fleas). In brief, the possible gradual loss of ectoparasites in small mammals is explained by the expansion of the host distributional range.

Several mechanisms have been suggested to cause nestedness in assemblages of free-living organisms, the most frequently cited are: selective extinction, selective immigration, nested habitats and passive sampling (Lomolino, 1996). Recently, other mechanisms have been tested through ecologically explicit null models of nestedness (Moore and Swihart, 2007). According to Rohde *et al*. (1998) differential colonization probabilities are the most likely cause of nestedness in parasite assemblages of marine fishes. Since the life cycle and the mechanisms of transmission of ecto- and endoparasites are different, the nested patterns (and/or richness latitudinal gradient) for those two groups of parasites could result from different processes affecting the parasite's colonization (González and Poulin, 2005; Guégan *et al*. 2005). In the present study, we observed latitudinal changes in the endoparasite richness of populations of marine fishes distributed along the southeastern Pacific coast. For instance, the endoparasite richness of *N. pulchella, P. chilensis* and *P. jugularis* tend to be higher in northern latitudes, whereas in *H. macrops* and *S. capensis* the endoparasite richness increased in southern latitudes. These latitudinal gradients in the endoparasite richness of the hosts might be explained by zoogeographical breaks of prey and/or by changes in prey availabilities (intermediate hosts) along host latitudinal range (González *et al*. 2006).

This study was funded by a Postdoctoral FONDECYT Project N°3060054 granted to the principal author. The authors thank Professor R. Poulin of the University of Otago and two anonymous referees for their critical comments on an early version of this manuscript.

REFERENCES

Atmar, W. and Patterson, B. D. (1993). The measure of order and disorder in the distribution of species in fragmented habitat. *Oecologia* **96**, 373–382.

Briggs, J. C. (1974). *Marine Zoogeography*. McGraw-Hill Co., New York, USA.

Bush, A. O., Lafferty, K. D., Lotz, J. M. and Shostak, A. W. (1997). Parasitology meets ecology in on its own terms: Margolis *et al*. revisited. *Journal of Parasitology* **83**, 575–583.

Bush, A. O., Fernández, J. C., Esch, G. W. and Seed, J. (2001). *Parasitism, the Diversity and Ecology of Animal Parasites*. Cambridge University Press, Cambridge, UK.

Escribano, R. and Hidalgo, P. (2001). Circulación inducida por el viento en Bahía de Antofagasta, norte de Chile (23°S). *Revista de Biología Marina y Oceanografía* **36**, 43–60.

Fischer, J. and Lindenmayer, D. B. (2005). Nestedness in fragmented landscapes: a case study on birds, arboreal marsupials and lizards. *Journal of Biogeography* **32**, 1737–1750.

González, M. T. and Acuña, E. (1998). Metazoan parasites of *Sebastes capensis* from northern Chile. *Journal of Parasitology* **84**, 753–757.

González, M. T. and Poulin, R. (2005). Nested patterns in parasite component communities of a marine fish along its latitudinal range on the Pacific coast of South America. *Parasitology* **131**, 569–571.

González, M. T. and Oliva, M. E. (2006). Similarity and structure in the ectoparasite communities of rockfish species from the southern Chilean coast. *Parasitology* **133**, 335–343.

González, M. T., Barrientos, C. and Moreno, C. A. (2006). Biogeographical patterns of endoparasite communities of a marine fish (*Sebastes capensis*) along its distributional range in Southern Hemisphere. *Journal of Biogeography* **33**, 1086–1095.

Gotelli, N. J. and Rohde, K. (2002). Co-ocurrence of ectoparasites of marine fishes: a null model analysis. *Ecology Letters* **5**, 86–94.

Goüy de Bellocq, J., Sarà, M., Casanova, J. C., Feliu, C., and Morand, S. (2003). A comparison of the structure of *Apodemus sylvaticus*, on islands of the western Mediterranean and continental Europe. *Parasitology Research* **90**, 64–70.

Guégan, J. F., Morand, S. and Poulin, R. (2005). Are there general laws in parasite community ecology? The emergence of spatial parasitology and epidemiology. In *Parasitism and Ecosystems* (ed. Thomas, F., Renaud, F. and Guégan, J.-F.), pp. 22–42. Oxford University Press, Oxford, UK.

Hayward, C. J. (1997). Distribution of external parasites indicates boundaries to dispersal of sillaginid fishes in the Indo-West Pacific. *Marine Freshwater Research* **48**, 391–400.

Holt, R. D. (2000). A biogeographical and landscape perspective on within-host infection dynamic. In *Proceedings of the 8th International Symposium of Microbial Ecology* (ed. Bell, C. R., Brylinsky, M. and Johnson-Green, P.), pp. 583–588. Atlantic Canada Society for Microbial Ecology, Halifax, Canada.

Krasnov, B. R., Shenbrot, G. I., Khokhlova, I. S. and Poulin, R. (2005). Nested pattern in flea assemblages across the host's geographic range. *Ecography* **28**, 475–484.

Kuris, A. M., Blaustein, A. R. and Alió, J. J. (1980). Hosts as islands. *American Naturalist* **116**, 570–586.

Lancellotti, D. A. and Vásquez, J. A. (1999). Biogeographical patterns of benthic macro-invertebrates in the Southeastern Pacific littoral. *Journal of Biogeography* **26**, 1001–1006.

Lomolino, M. V. (1996). Investigating causality of nestedness of insular communities: selective immigrations or extinctions? *Journal of Biogeography* **23**, 699–703.

Matejusová, I., Morand, S. and Gelnar, M. (2000). Nestedness in assemblages of gyrodactylids (Monogenea: Gyrodactylidae) parasitizing two species of cyprinid-with reference to generalists and specialists. *International Journal for Parasitology* **30**, 1153–1158.

Morand, S. and Poulin, R. (1998). Density, body mass and parasite species richness of terrestrial mammals. *Evolutionary Ecology* **12**, 717–727.

Morand, S., Rohde, K. and Hayward, C. (2002). Order in ectoparasite communities of marine fish is explained by epidemiological processes. *Parasitology* **124**, S57–S63.

Moore, J. E. and Swihart, R. K. (2007). Toward ecologically explicit null models of nestedness. *Oecologia* **152**, 763–777.

Ojeda, P., Labra, F. and Muñoz, A. (2000). Patrones biogeográficos de los peces litorales de Chile. *Revista Chilena de Historia Natural* **73**, 625–641.

Patterson, B. D. and Atmar, W. (1986). Nested subsets and the structure of insular mammalian faunas and archipelagos. *Biological Journal of the Linnaean Society* **28**, 65–82.

Pequeño, G. (1989). Peces de Chile. Lista sistemática revisada y comentada. *Revista de Biología Marina* (Chile) **24**, 1–132.

Poulin, R. (2004). Parasites and the neutral theory of biodiversity. *Ecography* **27**, 119–123.

Poulin, R. (2007*a*). Are there general laws in parasite ecology? *Parasitology* **134**, 763–776.

Poulin, R. (2007*b*). *Evolutionary Ecology of Parasites*. 2nd Edn. Princeton University Press, Princeton, NJ, USA.

Rohde, K. (2005). Zoogeography. In *Marine Parasitology* (ed. Rohde, K.), pp. 347–351. CABI Publishing, Oxford, UK.

Rohde, K., Worthen, W. B., Heap, M., Hugueny, B. and Guégan, J. F. (1998). Nestedness in assemblages of metazoan ecto-and endoparasites of marine fish. *International Journal for Parasitology* **28**, 543–549.

Sagarin, R. D. and Gaines, S. D. (2002). The "abundant centre" distribution: to what extent is it a biogeographical rule? *Ecology Letters* **5**, 137–147.

Silva, N. and Calvete, C. (2002). Características oceanográficas, físicas y químicas, de canales australes chilenos entre el golfo de Penas y el Estrecho de Magallanes (Crucero Cimar Fiordo 2). *Ciencia y Tecnología del Mar* (*Valpo.*) **25**, 23–88.

Timi, J. and Poulin, R. (2008). Different methods, different results: temporal trends in the study of nested subset patterns in parasite communities. *Parasitology* **135**, 131–138.

Ulrich, W. (2006). Nestedness- a FORTRAN program for calculating ecological matrix temperatures. http://www.uni.torun.pl/~ulrichw

Ulrich, W. and Gotelli, N. J. (2007*a*). Null model analysis of species nestedness patterns. *Ecology* **88**, 1824–1831.

Ulrich, W. and Gotelli, N. J. (2007*b*). Disentangling community patterns of nestedness and species co-occurrence. *Oikos* **116**, 2053–2061.

Wright, D. H., Patterson, B. D., Mikkelson, G. M., Cutler, A. and Atmar, W. (1998). A comparative analysis of nested subset patterns of species composition. *Oecologia* **113**, 1–20.

Zar, J. (1999). *Biostatistical Analysis*. Prentice-Hall Inc., NJ, USA.